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A LATE PLEISTOCENE HERPETOFAUNA FROM BELL CAVE, ALABAMA

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ABSTRACT

Three stratigraphic units in Bell Cave, northwestern Alabama, have yielded fossil herpetofaunas that are mainly analogues of the modern ones in the area. Two of the fossiliferous zones have been dated by the Carbon 14 method; Zone 1/2 at 11,820 +480 to –500 BP and Zone 4 at 26,500 +870 to –990 BP. An intermediate unit (Zone 3) did not yield a Carbon 14 date, but is faunistically nearly identical to Zone 1/2. Excessive damage was present in many of the fossils due to predators and gnawing scavengers, thus only 18 per cent of the 3,953 herpetological fossils could be identified to the generic or to the specific level. The wide variety of habitats represented by the fossils (small, clear streams; larger, slower streams; marshy wetlands; waterfalls and associated talus seeps; woodlands and woodland edges) is attributed to transportation by palaeopredators. None of the amphibian or reptile species is extinct, in contrast to the mammalian fauna which has several extinct taxa. Zone 1/2 has at least 24 species, including one northern and two slightly eastern extralimital ones. Zone 3 has at least 24 species, including the same three extralimital species that occur in Zone 1/2. Zone 4 has 13 species, including only two slightly eastern extralimital ones. It is difficult on the herpetological remains to suggest a palaeoclimate much different from the climate of the area today. Certainly, the presence of many egg-laying turtles, lizards and snakes in all units negates a tundra-like or boreal-like interpretation of the palaeoclimate.

INTRODUCTION

Late Wisconsinan faunas in midlatitude North America typically have extralimital, northern, mammalian species. This has led regularly to the conclusion that the climate was tundra-like or boreal-like. On the other hand, the herpetofaunas of these sites are usually similar or identical to those inhabiting such areas today, and this has led to an interpretive dilemma (Fay, 1984, 1986, 1988; Holman, 1986; Holman and Grady, 1987).

The lack of stratigraphic control in most of these faunas, many of them in caves, rock shelters, or fissure fillings, has led some workers to suspect that herpetological species were modern intrusives, and not contemporaneous with the mammalian species (references in Fay, 1988). Thus, the Bell Cave herpetofauna reported here is of considerable importance as it is from Carbon 14 dated, stratigraphically controlled, units. Moreover, it is the first large Pleistocene herpetofauna from Alabama.

The Bell Cave bone deposit lies in the NE corner of Section 9, Township 4 S, Range 12 W, 10.8k W of Tuscumbia, Colbert County, Alabama, 87° 47′ 45″ W, 34° 43′ 48″ N. The cave is located in a bluff, adjacent to the Tennessee River, within the Tuscumbia Limestone of Middle Mississippian age. It consists of a 26.2m horizontal crawlway which ends at a large, 4 by 11.9m oval, pit-like room.

This room acted as a settling basin for fissure-transported sediment, and has accumulated about 40cm of bone-packed mud. The deposit is distinctly separated into three bone-bearing units; Zone 1/2, Zone 3 and Zone 4, representing different depositional events. These units lie on top of a layer, at least 70cm thick, of sterile clay (Fig. 1). The sterile unit and its overlying bone-bearing unit (Zone 4) are both believed to have been subaqueously deposited. A lowering of the local water table resulted in the subsequent desiccation and consolidation of these two units and the onset of travertine formation. Zone 3 appears to have been deposited as a viscous mud flow from the fissure, and Zone 1/2 was deposited later in the same manner. Radiocarbon dates are as follows:

Zone 1/2 — 11,820 +480 to −500 BP (*Ursus americanus* femur)

Zone 3 — Not sufficient bone for a sample

Zone 4 — 26,000 +870 to −990 (various longbone fragments)

Matrix from each stratigraphic fossiliferous unit was collected in sacks and removed from the cave for processing. The matrix was dried and screened, mainly using the standard techniques of Hibbard (1949). The concentrate was then sorted into taxonomic groups. Nine different workers are studying the mammalian fossils of this rich site, greatly delaying the time of publication of that component of the cave fauna.

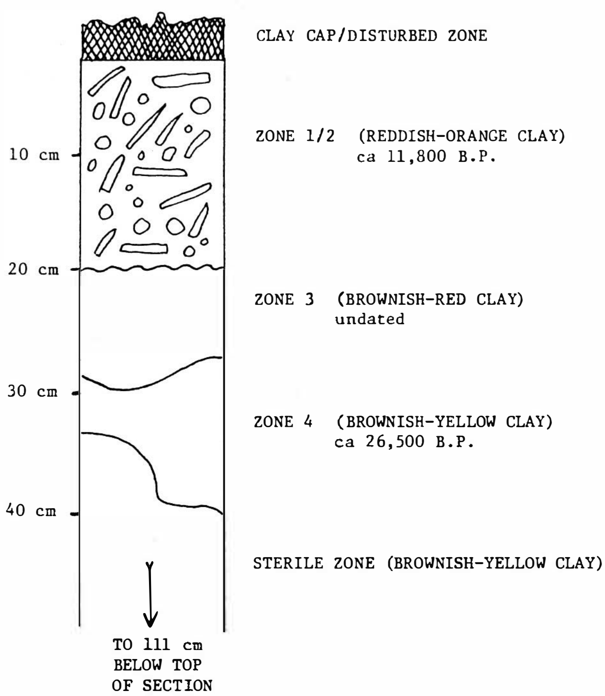

Fig. 1 Stratigraphic units of Bell Cave, Alabama, USA at Pit 1. The Clay Cap/Disturbed Zone is variable in thickness. Travertine slabs and large rounded pebbles are indicated in Zone 1/2.

SYSTEMATIC PALAEONTOLOGY

The fossils of this study are deposited in the Red Mountain Museum, Birmingham, Alabama, 35205, USA (abbreviated to RMM), and their collection numbers identify the specimens reported herein.

Class Amphibia

Order Caudata

Family Cryptobranchidae

Cryptobranchus alleganiensis (Daudin)

Hellbender

Zone 1: Pit 1, vertebra RMM 3943; Pit 3, left premaxilla 5081. Zone 1/2: Pit 1, atlas 3878, eight vertebrae 3858; Pit 2, atlas 4905, five vertebrae 4279; Pit 3, seven vertebrae 5057, six vertebrae 5079, vertebra 6764; Pit 4, 12 vertebrae 5264. Zone 3: Pit 1, right premaxilla 4806 (Fig. 2a), left maxilla 3999, three vertebrae 4320; Pit 3, nine vertebrae 4703 (Fig. 2b), vertebra 6675; Pit 4, five vertebrae 5348. Zone 4: Pit 2, atlas and three presacral vertebrae 4353 (Fig. 2c). Disturbed Zone: two vertebrae 3832 and 4047.

Holman (1977, 1982b) has discussed the identification of *Cryptobranchus alleganiensis* and *C. guildayi* on the basis of isolated bones. *Cryptobranchus alleganiensis* occurs in the Tennessee River System in northwestern Alabama today (Mount, 1975, Fig. 116). These animals are completely aquatic and occur in rocky streams with relatively clear water. Fossil hellbenders have been found in Pleistocene cave deposits in Virginia (Holman, 1986), West Virginia (Holman, 1982b; Holman and Grady, 1987) and Maryland (Holman, 1977).

Family Ambystomatidae

Ambystoma sp. indet.

Mole Salamander

Zone 1/2: Pit 1, 11 vertebrae RMM 4773; Pit 3, three vertebrae 5060; Pit 4, two vertebrae 5255. Zone 3: Pit 1, three vertebrae 4811, vertebra 6766; Pit 3, two vertebrae 4697; Pit 4, vertebra 5604.

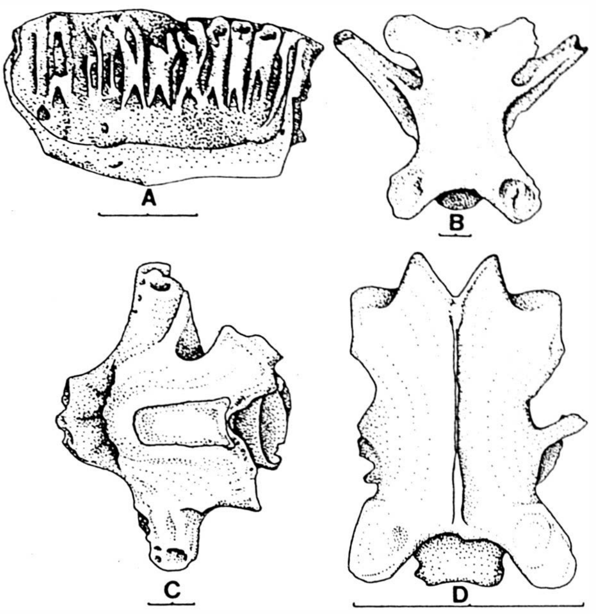

Fig. 2 Salamander fossils of Bell Cave. A. right premaxilla of *Cryptobranchus alleganiensis* RMM 4806; B. trunk vertebra of *C. alleganiensis* RMM 4703 in dorsal view; C. atlas of *C. alleganiensis* RMM 4553 in dorsal view; D. trunk vertebra of *Desmognathus ochrophaeus* RMM 6770 in dorsal view. Each scale line equals 2mm.

Tihen (1958) has given vertebral characters for the genus *Ambystoma*. The above vertebrae were too fragmentary for specific identification.

Ambystoma maculatum Shaw

Spotted Salamander

Zone 1/2: Pit 4, two vertebrae RMM 6767. Zone 3: Pit 1, vertebra 6768; Pit 3, vertebra 6769.

Tihen (1958) and Holman and Grady (1987) discuss the identification of *Ambystoma maculatum* on the basis of vertebrae. This animal occurs in the area today (Mount, 1975, Fig. 102) where it inhabits low areas where hardwood trees are present and pools are available for breeding.

Family Plethodontidae

Desmognathus sp. indet.

Dusky Salamander

Zone 4: Pit 4, vertebrae RMM 5606.

Holman and Grady (1987) have discussed the identification of this genus on the basis of vertebrae, but the above specimen is too fragmentary for specific identification.

Desmognathus ochrophaeus Cope

Mountain Dusky Salamander

Zone 4: Pit 1, vertebra RMM 6770 (Fig. 2d); Pit 4, two vertebrae 6771.

The identification of this species on the basis of vertebrae has been discussed by Holman and Grady (1987). A very deeply notched posterior end of the neural spine is characteristic of this species (Fig. 2d). Today, this species occurs in Alabama only in the extreme northeastern corner of the state (Mount, 1975, Fig. 127) where it occurs near moist cliff faces and talus areas beneath water falls.

Eurycea sp. indet.

Brook Salamander

Zone 1/2: Pit 4, vertebrae RMM 6772. Zone 4: (pit undesignated) five vertebrae.

Eurycea have amphicoelous or falsely opisthocoelous vertebrae that are slender; have a high, rounded or sometimes pointed neural spine; two small foramina behind the rib-bearers; and with the rib-bearers distinctly divided. We are unable to identify the above vertebrae specifically. Species of this genus occur in moist woodlands today.

Plethodon glutinosus (Green)

Slimy Salamander

Zone 1/2: Pit 1, vertebra RMM 6774; Pit 2, vertebra 4910. Zone 3: Pit 1, vertebra 6775. Overlying Clay Cap: 6776.

The identification of *P. glutinosus* middle trunk vertebrae was discussed by Holman and Grady (1987). The anterior trunk vertebrae of *P. glutinosus* also appear to be diagnostic in having a relatively short and wide form; with a well-developed, rounded neural spine; slender anterior zygapophyses; widely-spaced, cylindrical rib-bearers, two formamina anterior to the rib-bearers, a wide ventral surface; and with this surface with a constricted medial portion. This salamander occurs in the area today (Mount, 1975, Fig. 152) in many woodland habitats. All of the authors of this paper have seen living specimens in Bell Cave.

Order Anura

Family Bufonidae

Bufo sp. indet.

Zone 1: Pit 1, six sacra RMM 6677. Zone 1/2: Pit 1, one left and four right ilia 3780; Pit 2, left ilium 6778, sacrum 6779; Pit 3, sacrum 6780; Pit 4, sacrum 6781. Zone 3: Pit 3, three sacra 6782.

These elements were too fragmentary for specific identification.

Bufo americanus Holbrook

Zone 1/2: Pit 1, two left and one right ilia RMM 6783; Pit 2, left ilium 6784; Pit 3, right ilium 6785; Pit 4, right ilium 6788 (Fig. 3a). Zone 3: Pit 1, one left and two right ilia 6787; Pit 3, three left and one right ilia 6788, two left and two right ilia 6789.

The identification of isolated ilia of *B. americanus*, *B. terrestris* and *B. woodhousii* was detailed by Wilson (1975). The base of the ilial protuberance of *B. americanus* is wider than that of *B. woodhousii fowleri*. We have also noticed in skeletons of 12 *B. americanus* and 12 *B. w. fowleri* that the ilial protuberance is less distinctly marked from the prominence in *B. americanus* than in *B. w. fowleri*. *Bufo americanus* has not been recorded from northwestern Alabama today (Mount, 1975, Fig. 42), but it occurs in the northeastern part of the state. This species has ubiquitous habitats in basically woodland areas.

Bufo woodhousii fowleri Hinckley

Fowler's Toad

Zone 1/2: Pit 3, left ilium RMM 6790. Zone 3, left ilium 6791 (Fig. 3b), right ilium 6792.

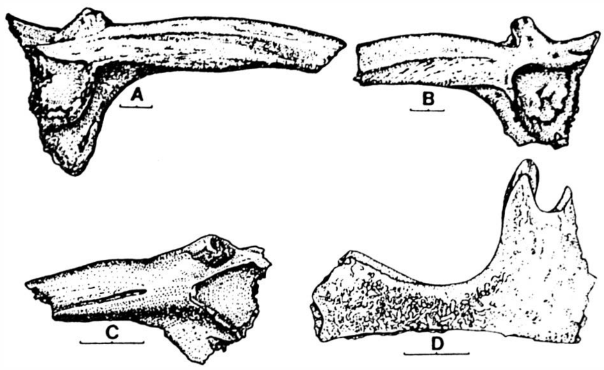

Fig. 3 Anuran and chelonian fossils of Bell Cave. A, right ilium of *Bufo americanus* RMM 6786 in lateral view; B, left ilium of *Bufo woodhousii fowleri* RMM 6791 in lateral view; C, left ilium of *Hyla gratiosa* RMM 6793 in lateral view; D, left hypoplastron of *Trionyx spiniferus* RMM 4580 in dorsal view. Scale lines A, B and C equal 2mm. Scale line D equals 20mm.

Bufo woodhousii fowleri is easily distinguished from its western counterpart *B. woodhousii woodhousii* on the basis of its much lower ilial protuberance. Fowler's toad occurs in the area today (Mount, 1975, Fig. 48). This species has ubiquitous habitats in basically woodland areas today.

Family Hylidae

Hyla gratiosa LeConte

Barking Treefrog

Zone 1: Pit 1, left and right ilia RMM 4767. Zone 1/2: Pit 4, left ilium 6793 (Fig. 3c).

Hyla gratiosa has an ilium that is distinguishable from other *Hyla* in being quite large; with an extensive ventral acetabular expansion; rounded dorsal protuberance that occurs posterior to the anterior edge of the acetabular cup; and with the protuberance close to the edge of the acetabular cup. There is a record of the barking treefrog quite near Bell Cave today (Mount, 1975, Fig. 62). This is a woodland treefrog.

Family Ranidae

Rana sp. indet.

Zone 1/2: Pit 1, sacrum RMM 6794. Zone 4: Pit 1, two sacra 6795; Pit 4, two sacra 6796.

These elements cannot be distinguished to species.

Rana pipiens complex

Leopard Frogs

Zone 1: Pit 1, left ilium RMM 4758, sacrum 6797. Zone 1/2: Pit 2, five left and four right ilia 6887; Pit 3, five left and two right ilia 6798; Pit 4, three right ilia 6799. Zone 3: Pit 1, left ilium and sacrum 4798, one left and two right ilia 6800; Pit 4, one left ilium 4595. Zone 4: Pit 1, four left and eight right ilia 6801; Pit 3, one left and one right ilia 5171, three left and 12 right ilia 6802, two left and two right ilia and one sacrum 6803; Pit 4, 22 left and 24 right ilia 6804. Overlying Clay Cap: right ilium 5544.

Characters for the identification of ilia of the *R. pipiens* complex are given in Holman (1984). Today, *R. palustris* and *R. sphenocephala* of this complex occur in the Bell Cave area (Mount, 1975, Figs. 93 and 95). Both species occur in marshy wetlands.

Rana catesbeiana Shaw

Bullfrog

Zone 1/2: Pit 3, right ilium RMM 5056.

Holman (1984) discussed the identification of ilia of *R. catesbeiana*. This species occurs in the area today (Mount, 1975, Fig. 84) in wetlands and streams.

Order Testudines

Trionyx sp. indet.

Zone 1: Pit 1, two carapace fragments RMM 4580. Zone 1/2: Pit 1, nine shell fragments 6805, 27 shell fragments 3709; Pit 2, 10 shell fragments 3633, 22 shell fragments 4858; Pit 3, 30 shell fragments 4952; Pit 4, 14 shell fragments 5185. Zone 3: Pit 1, 12 shell fragments 4186; Pit 3, two shell fragments 4723, 20 shell fragments 4644; Pit 4, 13 shell fragments 5341. Zone 4: Pit 1, one costal 4474, two shell fragments 4482; Pit 2, three shell fragments 4916; Pit 3, four shell fragments 5119. Disturbed Zone: one costal fragment 3779. Overlying Clay Cap: two shell fragments 5517, one shell fragment 5526.

These fossils were too fragmentary to identify to the specific level.

Family Trionychidae

Trionyx spiniferus Lesuer

Spiny Softshell Turtle

Zone 1: Pit 1, left hypoplastron RMM 4580 (Fig. 3d). Zone 1/2: Pit 2, one juvenile right hypoplastron 6808.

The hypoplastron of *T. spiniferus* is distinguished from that of *T. muticus* in having a much less acute greater xiphiplastral notch and a much shorter lesser xiphiplastral notch. This species occurs throughout Alabama today (Mount, 1975, Fig. 348), but there are no specific records near the cave site. This species occurs in rivers, lakes, and permanent ponds.

Family Emydidae

Chrysemys picta (Schneider)

Zone 4: Pit 1, nuchal and left epiplastron RMM 6807. Ledge in Fissure: right hypoplastron 4539 (Fig. 4a).

The serrated anterior end of the nuchal scute area of the nuchal bone appears to be diagnostic in many individuals of this species. The hypoplastron of *C. picta* differs from that of *Pseudemys concinna*, *P. floridana* and *Trachemys scripta* in having the inguinal scute shorter and broader. This bone further differs from *T. scripta* in its smoother texture, smaller size and more vertically directed inguinal buttress. This species occurs in the area today (Mount, 1975, Fig. 297) in ponds, lakes and slowly moving streams with soft bottoms and abundant aquatic vegetation.

Graptemys geographica (Le Sueur)

Common Map Turtle

Zone 1/2-3: Pit 5, lower mandible of a female and three peripherals RMM 6888.

The lower mandible of female *G. geographica* differs from the male of *G. geographica*, and from both sexes of the sympatric *G. pseudogeographica* in having the posterior part of the crushing surface of each dentary

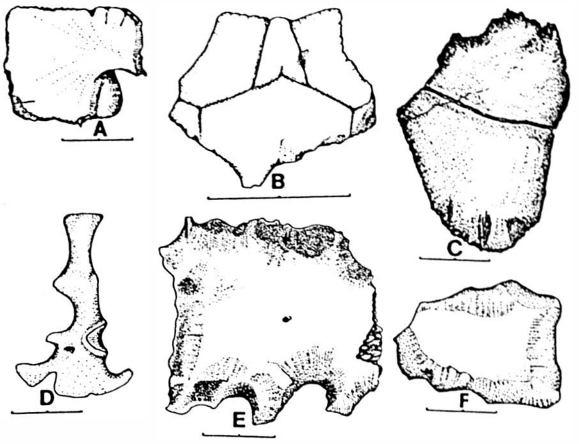

Fig. 4 Chelonian and lizard fossils of Bell Cave. A, right hypoplastron of *Chrysemys picta* RMM 4539 in dorsal view; B, nuchal bone of *Pseudemys concinna* RMM 6813 in dorsal view; C, left xiphiplastron of *P. concinna* RMM 6814 in ventral view; D, left scapulocoracoid of *Anolis carolinensis* RMM 4822 in lateral view; E, indeterminate emydid turtle plastron RMM 3724 (in dorsal view) that had been crushed by a large predator; F, indeterminate emydid turtle plastron RMM 5184 (in dorsal view) that had been gnawed by rodents. Scale lines A, B, C, E and F equal 20mm. Scale line D equals 2mm.

broadly expanded posteriorly as a mollusk-crushing specialisation. *G. geographica* occurs in the area today (Mount, 1975, Fig. 305) in rivers, creeks and brooks.

Pseudemys sp. indet.
Cooters and Red-bellied Turtles

Zone 1/2: Pit 1, left hypoplastron RMM 6810; Pit 2, right hyoplastron 6811. Disturbed Zone: right hypoplastron 3690.

These bones are too damaged by predators to identify to species.

Pseudemys concinna (Le Conte)
River Cooter

Zone 1/2: Pit 1, two right hyoplastra RMM 6812; Pit 3, two right hypoplastra 4445. Zone 3: Pit 3, nuchal 6813 (Fig. 4b), left xiphiplastron 6814 (Fig. 4c).

The nuchal of *P. concinna* appears to be separable from other emydid turtles of southeastern United States, having a triangular nuchal scute that is about twice as long as it is high, and that is slightly upraised; no sculpturing on the dorsal surface of the bone; and the anterior edge of the bone slightly indented. The hypoplastron of *P. concinna* has the inguinal longer and narrower than in *C. picta* and *T. scripta* and less etched into the bone than in *Pseudemys floridana*. The xiphiplastron *P. concinna* has its posterior end more narrowly rounded than in *C. picta*, *P. floridana* or *P. scripta*. *P. concinna* occurs in the area today (Mount, 1975, Fig. 323) where it is said to prefer streams and large lakes.

Order Squamata
Family Iguanidae
Anolis carolinensis Voigt
Green Anole

Zone 4: Pit 1, left scapulocoracoid RMM 4822 (Fig. 4d).

Although the scapulocoracoid of lizards has been infrequently reported in the fossil record, this element appears to be diagnostic. This is probably because of its complex structure (Romer, 1956) that probably reflects differences in posture and locamotion. This element in *A. carolinensis* is very distinct from those of other lizards of the eastern United States. The complex of processes on the anterior face of the bone as well as the position of the lateral nutrient foramen and relationship of the posteroventral process to the acetabulum (Fig. 4d) are all distinct and diagnostic characters.

The species occurs almost anywhere that vegetation and shade are abundant in Alabama today (Mount, 1975).

Family Colubridae
Carphophis amoenus (Say)
Worm Snake

Zone 1/2: Pit 4, three vertebrate RMM 6815. Zone 3: Pit 1, two vertebrate 6816. Zone 4: Pit 4, two vertebrae 6817. Disturbed Zone: one vertebra 6818. Clay Cap: Pit 3, one vertebra 6819.

Holman and Grady (1987) give characters that distinguish the vertebrae of *C. amoenus* from those of the very similar *Diadophis punctatus*. The worm snake occurs in the area today (Mount, 1975, Fig. 195), in open woodlands and woodland edges, and is frequently discovered near *Diadophis punctatus*.

Coluber constrictor Linnaeus
Black Racer

Zone 3: Pit 1, one vertebra RMM 6820; Pit 3, one vertebra 6821; Pit 4, one vertebra 6822.

Holman (1981) gave references to publications that discussed the identification of *C. constrictor* on the basis of individual fossil vertebrae. The black racer occurs in the area today (Mount, 1975, Fig. 200) in open woodland and forest edges, as well as along brushy steam edges.

Diadophis punctatus (Linnaeus)
Ringneck Snake

Zone 3: Pit 1, one vertebra RMM 6823.

Holman and Grady (1987) give characters that distinguish the vertebrae of *D. punctatus* from the similar *Carphophis amoenus*. *Diadophis punctatus* occurs in the area today (Mount, 1975, Fig. 202) where it is often found in the vicinity of *Carphophis amoenus*.

Elaphe sp. indet.
Ratsnake

Zone 1/2: Pit 1, nine vertebrae RMM 6824; Pit 2, one vertebrae 6825; Pit 3, one vertebra 6826. Zone 3: Pit 1, one vertebra 4099, one vertebra 4300; Pit 3, one vertebra 6827; Pit 4, three vertebrae 6828.

These vertebrae are too fragmentary for specific identification.

Elaphe cf. *Elaphe guttata* (Linnaeus)
Cornsnake

Zone 1/2: Pit 2, one vertebra RMM 6829.

Auffenberg (1963) discusses the identification of isolated vertebrae of species of *Elaphe*. This vertebrae fits his criteria for *E. guttata* in most respects, including the height of the neural spine. On the basis of having only a single vertebra, we are tentatively referring the fossil to *E. guttata*. This species occurs in the area today (Mount, 1975, Fig. 206) where it is frequently found near woodland edges.

Elaphe vulpina Baird and Girard

Foxsnake

Zone 1/2: Pit 1, one vertebra RMM 6830; Pit 2, one vertebra 6831. Zone 3: Pit 1, two vertebrae 6832; Pit 4, one vertebra 6833.

This snake gets no closer to the area today than northeastern Missouri and southwestern Illinois (Conant, 1975, map 148).

Vertebral characters of this snake are given in Holman (1982a). This species is one of the most easily identified large colubrid snakes in North America based on individual vertebrae. The foxsnake had a much wider distribution in the eastern and southeastern United States in the Pleistocene than it has today (Holman, 1981, 1984); it has recently been recorded from the late Pleistocene of Georgia (Holman, 1985a,b). This species is found in grasslands and woodland edges.

Heterodon cf. Heterodon platirhinos Latreille

Eastern Hognose Snake

Zone 1/2: Pit 1, two vertebrae RMM 6834; Pit 2, one vertebra 6835. Zone 3: Pit 1, three vertebrae 6836; Pit 3, three vertebrae 6837. Zone 4: Pit 1, two vertebrae 6838.

Holman (1981) quotes literature that deals with the identification of vertebrae of the species of *Heterodon*. Mount (1975) considers this species to be of statewide occurrence in Alabama, in areas of broken terrain.

Lampropeltis getulus (Linnaeus)

Eastern Kingsnake

Zone 1/2: Pit 3, one vertebra RMM 6839. Zone 3: Pit 4, one vertebra 6840. Zone 4: Pit 1, one vertebra 6841.

Holman (1981) quotes references to the identification of isolated vertebrae of this species. The eastern kingsnake occurs in the area today (Mount, 1975, Fig. 223) at the edges of aquatic habitats.

Lampropeltis triangulum triangulum (Lacepede)

Northern Milksnake

Zone 1/2: Pit 1, five vertebrae RMM 6842; Pit 4, one vertebra 6843. Zone 3: Pit 1, six vertebrae 6844; Pit 3, seven vertebrae 6845; Pit 4, four vertebrae 6846. Zone 4: Pit 3, three vertebrae 6847; Pit 4, 25 vertebrae 6848.

The identification of this large subspecies based on individual vertebrae is discussed in Holman (1985a). The northern milksnake occurs only in extreme northeastern Alabama today (Mount, 1975, Fig. 227) where it is a secretive woodland form.

Nerodia sp. indet.

Watersnake

Zone 1/2: Pit 1, 18 vertebrae RMM 6849; Pit 2, four vertebrae 6850; Pit 3, one vertebra 6851; Pit 4, two vertebrae 6852. Zone 3: Pit 4, six vertebrae 6853.

These vertebrae are too fragmentary to identify to the specific level.

Nerodia sipedon (Linnaeus)

Northern Watersnake

Zone 1/2: Pit 1, one vertebra RMM 6854; Pit 3, three vertebrae 6855; Pit 4, five vertebrae 6856. Zone 3: Pit 1, one vertebra 6857; Pit 3, two vertebrae 6858; Pit 4, two vertebrae 6859. Zone 4: Pit 4, six vertebrae 6860.

Brattstrom (1967) and Holman (1967) discuss the identification of *Nerodia* and species of *Nerodia* on the basis of isolated vertebrae. The species occurs in the area today (Mount, 1975, Fig. 246) in a variety of aquatic habitats.

Opheodrys aestivus (Linnaeus)

Rough Green Snake

Zone 1/2: Pit 1, two vertebrae RMM 6861; Pit 3, one vertebra 6862. Zone 3: Pit 4, six vertebrae 6863.

Holman and Richards (1981) distinguish between vertebrae of *O. aestivus* and *O. vernalis*. *Opheodrys aestivus* is found in the area today (Mount, 1975, Fig. 250) where it is common in vegetation around lakes and streams.

Storeria sp. indet.

Brown or Redbelly Snake

Zone 1/2: Pit 1, three vertebrae RMM 6864; Pit 3, one vertebra 6865; Pit 4, 11 vertebrae 6866. Zone 3: Pit 1, two vertebrae 6867; Pit 3, two vertebrae 6868; Pit 4, six vertebrae 6869.

Holman (1981) gives references for the identification of *Storeria* vertebrae. We cannot determine the species of the above vertebrae. Mount (1975) believes that the two species of *Storeria* that occur in Alabama today (*S. dekayi* and *S. occipitomaculata*) occur statewide.

Thamnophis sp. indet.

Garter or Ribbon Snake

Zone 1/2: Pit 1, 19 vertebrae RMM 6870; Pit 2, three vertebrae 6871; Pit 3, one vertebra 6872; Pit 4, two vertebrae 6873. Zone 3: Pit 1, nine vertebrae 4812; Pit 3, seven vertebrae 6874; Pit 4, four vertebrae 6875. Zone 4: Pit 1, one vertebra 6876.

Brattstrom (1967) discusses the identification of isolated *Thamnophis* vertebrae. These fossils are too fragmentary for specific identification.

Thamnophis sirtalis (Linnaeus)

Gatersnake

Zone 1/2: Pit 1, seven vertebrae RMM 6877; Pit 3, one vertebra 6878. Zone 3: Pit 3, one vertebra 6879. Zone 4: Pit 1, one vertebra 6880.

Holman (1984) has discussed how vertebrae of large *T. sirtalis* may be separated from those of the similar *T. proximus* and *T. sauritus*. Mount (1975) considers *T. sirtalis* to occur statewide in Alabama.

Family Viperidae

Agkistrodon sp. indet.

Copperhead or Cottonmouth

Zone 4: Pit 3, one vertebra RMM 6882.

Holman (1981) gives references for the identification of *Agkistrodon* and *Crotalus* vertebrae. We are unable to determine this broken vertebra to the specific level.

Crotalus horridus Linnaeus
Timber Rattlesnake

Zone 1/2: Pit 2, one vertebra RMM 6883; Pit 3, five vertebrae 5055. Zone 3: Pit 1, two vertebrae 6884, one vertebra 4195, one vertebra 6885; Pit 3, nine vertebrae 4638. Zone 4: Pit 1, one vertebra 4142, two vertebrae 6886; Pit 3, four vertebrae 5173.

Holman (1967) gives characters that distinguish *C. horridus* from other viperid species in eastern United States. This species is considered by Mount (1975) to have a statewide occurrence in Alabama today. The timber rattlesnake is a species that prefers forested areas, especially if rocky ledges are available for hibernation.

DISCUSSION

Herpetological evidence from late Wisconsinan cave faunas in the United States has sometimes been neglected or misinterpreted (Holman, 1986; Fay, 1988). Several of these faunas have amphibian and reptile species that would not be ecologically compatible with some of the mammalian species today; but some workers have disregarded these herpetological species on the supposition that they were modern intrusions into the fauna. But the Bell Cave herpetofauna is temporally in context with the rest of the fauna. Moreover, Carbon 14 dates in identifiable stratigraphic units provide a stratigraphic control that is unusual in some previously reported North American Pleistocene cave faunas.

Excessive damage was present on many of the fossil bones due to the activities of predators and scavengers. Thus, only 718 of 3953 individual bones (18 per cent) were identified to the generic or to the specific level. Fig. 4e,f shows two turtle bones that could not be identified to genus or species. Fig. 4e is from the plastron of a large emydid turtle that had been bitten by a very large predator. Emmons (1989) has detailed how jaguars (*Planthera onca*) feed upon turtles by crushing the shells in their jaws. It is likely that many of the large turtle remains from the Ladds, Georgia, USA, Pleistocene site had been crushed by these large-headed felines (Emmons, 1989, Fig. 1; Holman, 1985a, Fig. 4). It therefore seems possible that the large tooth marks on the Bell Cave, Alabama, turtle shells could also have been made by *Panthera onca*. Fig. 4f is from the plastron of a smaller emydid turtle that had been gnawed by rodents.

A wide variety of aquatic and terrestrial habitats is indicated by the fossil herpetofauna, and this may be most logically attributed to transportation of prey to the cave by various predators. Bears and large felids (still being studied) were present in the cave as attested by fossil remains.

Small clear streams are indicated by *Cryptobranchus alleganiensis*. Larger, slower streams are indicated by *Chrysemys picta*, *Graptemys geographica*, *Pseudemys concinna*, *Trionyx spiniferus*, and *Nerodia sipedon*. Marshy wetlands are indicated by *Rana catesbeiana*, *Rana pipiens* complex, *Storeria* sp. and *Thamnophis sirtalis*. Talus areas below waterfalls or seeps are indicated by *Desmognathus ochrophaeus*. Woodlands and woodland edges are indicated by *Ambystoma maculatum*, *Eurycea* sp., *Plethodon glutinosus*, *Bufo americanus*, *Bufo woodhousii fowleri*, *Hyla gratiosa*, *Anolis carolinensis*, *Carphophis amoenus*, *Coluber constrictor*, *Diadophis punctatus*, *Elaphe* cf. *E. guttata*, *Elaphe vulpina*, *Heterodon* cf. *H. platirhinos*, *Lampropeltis getulus*, *Lampropeltis t. triangulum*, *Opheodrys aestivus* and *Crotalus horridus*.

All of the fossil amphibians and reptiles from the Pleistocene of Bell Cave are represented by species that are living today, a situation that is not unusual in North American late Wisconsinan herpetological assemblages. This is in sharp contrast to North American late Wisconsinan mammalian assemblages which suffered much extinction at the end of the Pleistocene. Extinct felids, cervids, armadillos and horses, as well as smaller mammals, were recovered from Bell Cave and are currently being studied by several experts on the various taxonomic groups.

The absence of the extinct giant land tortoise, *Geochelone crassiscutata*, which was present in the late Wisconsinan fauna of northwestern Georgia, USA, (Holman, 1985a,b) is unexplained, but could be related to some unknown or uninterpreted taphonomic event. The lack of extinction in the North American herpetofauna during the past 1.8 million years compared to that of the mammals, and to a lesser extent, the birds, is becoming a subject of considerable discussion (Holman, 1989).

Bell Cave is typical of several late Wisconsinan faunas (Fay, 1984, 1986, 1988; Holman, 1986; Holman and Grady, 1987) in having a herpetofauna that resembles the modern one in the area. The relative stability of these herpetofaunas in the face of the changes that occurred in the late Pleistocene has posed a problem that has been discussed, but not actually resolved (Holman, 1986; Holman and Grady, 1987; Fay, 1988).

We have no reason to believe that there has been a systematic misidentification of taxa from these sites. Moreover, several of these faunas are from caves with beds that are very well stratified and that have been dated by the Carbon 14 method (Holman, 1986; Holman and Grady, 1987; Fay, 1988). Therefore, there is every reason to believe that all of the fossil vertebrate taxa from these sites were living contemporaneously.

Thus, the most parsimonious explanation for these seemingly disharmonious assemblages appears to be the one proposed in reference to the late Pleistocene vertebrate fauna of New Trout Cave, West Virginia by Holman and Grady (1987). This hypothesis was *that somewhat cooler summers and a more mosaic vegetation would allow for the selective survival of some of the mammalian species that were forced southward by the advancing glacial front; and that the presence of northern amphibian and reptile populations forced southward would not be easily detected because of the lack of herpetological species with restrictive northern distributions.*

The Ladds herpetofauna of northwestern Georgia (Holman, 1985a,b) remains an exceptional one, having striking northern and southern extralimital species from coevel Carbon 14 dated late Wisconsinan

TAXON	*ZONE 1/2*	*ZONE 3*	*ZONE 4*
Cryptobranchus alleganiensis	X	X	X
Ambystoma sp. indet.	X	X	
Ambystoma maculatum	X	X	
Desmognathus sp. indet.			X
Desmognathus ochrophaeus			X
Eurycea sp. indet.	X		X
Plethodon glutinosus	X	X	
Bufo sp. indet.	X	X	
Bufo americanus	X	X	
Bufo woodhousii fowleri	X	X	
Hyla gratiosa	X		
Rana sp. indet.			X
Rana pipiens complex	X	X	X
Rana catesbeiana		X	
Trionyx sp. indet.	X	X	
Trionyx spiniferus	X		
Chrysemys picta			X
Graptemys geographica	X	X	
Pseudemys sp. indet.	X		
Pseudemys concinna	X	X	
Anolis carolinensis			X
Carphophis amoenus	X	X	
Coluber constrictor		X	
Diadophis punctatus		X	
Elaphe sp. indet.	X	X	
Elaphe cf. *E. guttata*	X		
Elaphe vulpina	X	X	
Heterodon cf. *H. platirhinos*	X	X	X
Lampropeltis getulus	X	X	X
Lampropeltis t. triangulum	X	X	X
Nerodia sp. *indet.*	X	X	
Nerodia sipedon	X	X	X
Opheodrys aestivus	X	X	
Storeria sp. indet.	X	X	
Thamnophis sp. indet.	X	X	X
Thamnophis sirtalis	X	X	X
Agkistrodon sp. indet.			X
Crotalus horridus	X	X	X

TABLE 1: Pleistocene amphibians and reptiles of Bell Cave, Alabama

fissures. An explanation for the anamolous Ladds fauna is still being sought.

Table 1 indicates the distribution of fossil amphibian and reptile species by stratigraphic zone at Bell Cave. Zone 1/2 has a Carbon 14 date of about 12,000 B.P., thus the bones were deposited during the restoration of interglacial conditions that lasted from about 15,000 to about 10,000 B.P. in North America (Watts, 1983). Zone 3 does not have a Carbon 14 date, but it has a similar sedimentary profile and is faunistically very similar to Zone 1/2 (Table 1).

Twenty-four species occur both in Zone 1/2 and Zone 3; and the same extralimital species (*Bufo americanus*, *Elaphe vulpina* and *Lampropeltis t. triangulum*) are present in both zones. *Bufo americanus* and *Lampropeltis t. triangulum* occur only in the northeastern tip of Alabama today, but *Elaphe vulpina* gets no closer to the vicinity of the cave today than northeastern Missouri and southwestern Illinois. But *E. vulpina* had a much wider distribution in the east and southeast in the Pleistocene (Holman, 1981) and has been recorded from the late Wisconsinan fauna of northwestern Georgia (Holman, 1985a,b). These slightly eastern species and the northern species might be interpreted as suggesting a somewhat moister and/or cooler palaeoclimate. But the fauna as a whole does not suggest a climate much different than occurs in the area today. Most certainly, the presence of egg-laying reptiles (*Pseudemys concinna*, *Trionyx spiniferus*, *Carphophis amoenus*, *Coluber constrictor*, *Diadophis punctatus*, *Elaphe* cf. *E. guttata*, *Elaphe vulpina*, *Heterodon* cf. *H. platirhinos*, *Lampropeltis t. triangulum*, and *Opheodrys aestivus*) negates a Tundra-like or

Boreal-like climate during the deposition of the bones in Zones 1/2 and 3.

Zone 4 has a Carbon 14 date of about 26,000 B.P., thus the bones were deposited during the first part of a climatic deterioration that began 30,000 years ago and that culiminated in the glacial maximum in North America about 18,000 years ago (Watts, 1983). Of the 13 species identified from Zone 4, two are extralimital: *Desmognathus ochrophaeus* and *Lampropeltis t. triangulum*, both occur only in the tip of northwestern Alabama today. Again, the fauna does not suggest a climate much different than occurs in the area of the cave today.

Also, the presence of egg-laying reptiles (*Chrysemys picta*, *Anolis carolinensis*, *Heterodon* cf. *H. platirhinos*, *Lampropeltis getulus* and *Lampropeltis t. triangulum*) and especially *Anolis carolinensis*, a species very vulnerable to cold (Mount, 1975) negates the possibility of a Tundra-like or Boreal-like climate during the deposition of the bones in Zone 4.

CONCLUSIONS

Late Wisconsinan herpetofaunas from the middle latitudes of North America usually are very similar to the herpetofaunas that occur in the vicinity of the fossil localities today, whereas the fossil mammalian fanuas from these localities usually have many extralimital and extinct taxa. The Bell Cave herpetofauna fits this pattern. Many of the fossil amphibian and reptile bones were badly damaged by predators and scavengers, and the wide variety of habitats represented by the amphibian and reptile species is attributed to transportation by palaeopredators. It is difficult to suggest a palaeoclimate much different from the climate of the area today based on the herpetologic remains from any of the stratigraphic units in Bell Cave. Certainly, the presence of many egg-laying turtles, lizards and snakes in all units negates a Tundra-like or Boreal-like interpretation of the paleoclimate.

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